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IDENTIFICATION OF BIRD SUBFOSSILS FROM CAVE SURFACE DEPOSITS AT ANJOHIBE, MADAGASCAR, WITH A DESCRIPTION OF A NEW GIANT *COUA* (CUCULIDAE: COUINAE)

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Abstract.—A collection of bird subfossils from cave surface deposits in northwestern Madagascar is described. The majority of specimens represent taxa that still occur in the region. The exception is a partial pelvis referable to the genus *Coua* (Cuculidae: Couinae), but which is considerably larger than any known species. This specimen is described as a new species.

Résume.—Une collection d'ossements subfossiles d'oiseau provenant des gisements cavernicoles de surface du Nord-Ouest de Madagascar a été décrite. La plupart des spécimens représentant des taxons qui'existent encore dans la région. La seule exception est constitueé par un bassin incomplet pouvant se rapporter au genre *Coua* (Famille Cuculidae: sous-famille Couinae), mais qui est nettement plus grand que toute espèce connue. Ce spécimen est décrit comme nouvelle espèce.

Famintinana.—Nofantarina ireo tahirina taratsiefan-taolam-borona hita tany amin'ireo sompitrakoran-johy amin'iny faritra avaratr'andrefan'i Madagasikara iny. Ny ankamaroan'ireo santiona azo dia tsy hafa noho ireo karazana mbola fahita ao am-paritra. Ny hany niavaka tamin'ireo dia ilay sila-taola-maoja iray izay azo raisina ho an'ny sokajy *Coua* (Tarika Cuculidae: zanatarika Couinae), saingy lehibe lavitra noho izay karazana rehetra fantatra ho misy. Naraikitra ho karazana vaovao ity santiona ity.

The subfossil fauna of Madagascar is well known for its remarkable array of lemurs (e.g., Vuillaume-Randriamanantena 1982, Simons et al. 1990) and elephant birds (Aepyornithiformes) (Andrews 1894, Lamberton 1934, Battistini 1965). The study of hundreds of animal bones recovered at various sites on Madagascar has provided insight into the Holocene faunas of the island, inference about ecological change, as well as the reasons that a portion of these taxa have gone extinct in the past few thousand years (Dewar 1984, MacPhee 1986). In parallel situations on other islands, subfossil bird bones have provided important information about paleoenvironments and the effects of anthropogenic perturbations (Steadman 1989, James & Olson 1991, Olson & James 1991). While there are numerous archaeological sites on Madagascar that have yielded bird bones, this material with the exception of elephant birds has been rarely studied and thus not synthesized into the current working knowledge of the Holocene environment of the island.

In 1983 and 1986 excavations were carried out in northwestern Madagascar near Mahajanga in the Grottes d'Anjohibe (Andranoboka), by the Laboratoire de Primatologie et de Paléontologie des Vertébrés, Service de Paléontologie, Université d'Antananarivo (formerly Université de Madagascar), and Duke University Primate Center. The focus of these studies was primates (Vuillaume-Randriamanantena et al. 1985, Simons et al. 1990), but a wide array of other animal remains were recovered. During the 1986 field season approximately 1100 whole or fragmented subfossil bones of non-primate vertebrates were excavated, and, excluding the bird material, these have been described by Ravoavy (1991). In this paper we present information on 94 specimens of avian bones recovered during the 1983 and 1986 field seasons at Anjohibe.

Description of Site

Anjohibe is located in Mahajanga Province, approximately 80 km NE of Mahajanga, and is part of a series of caves generally referred to as the Grottes d'Andranoboka (Decary 1938, de Saint-Ours & Paulian 1953). One cave in particular is called the Grotte d'Anjohibe (de Saint-Ours 1953). The surface material described herein was collected in the northern end of de Saint-Ours & Paulian's (1953) "Grotte Principale no. 1" (Ravoavy 1991).

The cave is over 1200 m long from north to south, and with floor to ceiling heights in some places exceeding 12 m. There are numerous entrances and side passages to the cave. It still has "active" calcite formations (de Saint-Ours & Paulian 1953), and has been used in recent times by local people for a variety of activities (de Saint-Ours 1953).

All of the material collected during the 1983 and 1986 seasons was from surface deposits (MacPhee et al. 1984; E. Simons, pers. comm.). Bone is washed into the cave by floods during the rainy season. Also, some animals fall through aven, which are straight vertical holes open from the ground surface down to the cave floor as much as 60 m below. There is also a portion of the cave where the ceiling has collapsed (area M of de Saint-Ours & Paulian 1953) and forest vegetation is found on the floor of the cave. No radiocarbon date has been determined for any of the material recovered from the cave (Godfrey & Vuillaume-Randriamanantena 1986; E. Simons; pers. comm.). Thus, we have no idea when the material was deposited, or the span of years represented. Most of the bird bones show no signs of permineralization and are probably comparatively recent in age. The only exception is a *Coua* pelvis which has some surface mineralization, although the underlying structure is bone, and thus may be older than the balance of the material.

Table 1.—Bird species and minimum number of individuals identified from bones recovered during the 1983 and 1986 field seasons at Anjohibe. Excludes material of *Coua berthae.*

Taxa	Minimum number of individuals	
	1983	1984
Buteo brachypterus	1	
Falco newtoni		1
Coturnix sp.		2
Numida meleagris	2	4
Turnix nigricollis		2
Coracopsis vasa		1
Tyto alba		2
Otus rutilus		2
Merops superciliosus		1
Hypsipetes madagascariensis	1	1
Foudia madagascariensis		1

Birds Recovered from the Surface Deposits

A total of 12 and 82 bird bones recovered during the 1983 and 1986 field seasons (respectively) was used in this study. Most of the species identified (Table 1) are taxa that still occur in the area (Langrand 1990). The present natural vegetation of the region is dry deciduous forest; considerable portions of this habitat have been degraded in the past few centuries. The majority of birds identified from the surface deposits are species associated with open habitats and/or the forest edge. The hawk (*Buteo brachypterus*), falcon (*Falco newtoni*), parrot (*Coracopsis vasa*), and owl (*Tyto alba*) presently occur in a variety of habitats from grassland savanna to wooded environments. A partially unossified mid-shaft of a humerus, referable to *Tyto,* was a young individual probably incapable of sustained flight, and this species almost certainly bred in the cave. The falcon may have roosted or even nested in the cave. The presence of these two raptors in the cave would account for some of the small mammal and amphibian bones recovered from the ground surface of the cave (Ravoavy 1991); these would have been originally deposited as regurgitated pellets. The guineafowl (*Numida meleagris*), buttonquail (*Turnix nigricollis*), quail (*Coturnix* sp.), bee-eater (*Merops superciliosus*), and fody (*Foudia madagascariensis*) are generally found in grassland savanna, while a second species of owl (*Otus rutilus*) and a bulbul (*Hypsipetes madagascariensis*) occur in woodland areas or along the forest edge. Of these species, *Turnix, Merops, Hypsipetes,* and *Foudia* have been identified from *Tyto alba* pellets collected on Madagascar (Langrand & Raxworthy, pers. comm.).

The most common bird species recovered from these surface deposits was *Numida.* Adults of this species weigh over 1100 g (Urban et al. 1986) and are too heavy to have been carried into the cave by any raptor known to occur on the island. *Numida* may have been introduced to Madagascar, and it is now extensively hunted on the island by people (Langrand 1990). There was no clear sign of carnivore gnawing, butchering marks nor charring on the *Numida* bones, nor on any of the other bird material recovered from the cave. It is not clear what agent(s) was (were) responsible for the deposition of these bones in the cave. On a few occasions during the excavations *Numida* were observed flying in and out of the cave in an area with a collapsed ceiling and extensive vegetation. Thus, the *Numida* bones recovered from the surface deposits may be of individuals that naturally died within the cave.

One bone, a pelvis, from the 1983 collection cannot be identified to any modern species. On the basis of numerous osteological characters, the bone belongs to an exceptionally large coua (*Coua*), a subfamily of cuckoos (Cuculidae: Couinae) endemic to Madagascar. There are nine extant *Coua* spp. on the island. *Coua caerulea, reynaudii,* and *serriana* are found in humid forests; *gigas, cursor, ruficeps,* and *verreauxii* in the dry thorn scrub or dry deciduous forests; and *cristata* and *coquereli* in both wet and dry forest types (Langrand 1990). A tenth species, *C. delalandei,* once occurred on Ile Sainte Marie, 8 km off the northeastern coast of Madagascar, and possibly on the main island itself, but has gone extinct in the past 150 years (Langrand 1990, Goodman 1993). *Coua delalandei* and *gigas* are the largest known recent couas, measuring approximately 57 and 62 cm (respectively) in total length (Langrand 1990).

Milne-Edwards & Grandidier (1895) described an undated subfossil tarsometatarsus as a new species, *Coua primavea,* which was excavated from a deposit on the west coast of Madagascar at Belo-sur-mer, south of Morondava, and about 660 km south of Anjohibe. They distinguished the subfossil from other modern couas by its size; the tarsometatarsus of *primavea* measured 84 mm in total length, *delalandei* 70 mm, and *gigas* 69 mm (the latter two measurements are presumably from skin specimens). We have examined the type tarsometatarsus of *primavea* (Muséum National d'Histoire Naturelle, Service de Paléontologie, Paris, registration MAD 7078) and it measures 83.2 mm in total length. On the basis of a regression analysis between tarsometatarsus and pelvis length of modern couas and *primavea* (see Discussion), the pelvis recovered from Anjohibe cannot be referred to any known species of *Coua* and we propose to call it:

Coua berthae, new species
Figs. 1, 2

Holotype.—Left half of pelvis, collections of the Laboratoire de Primatologie et de Pa-

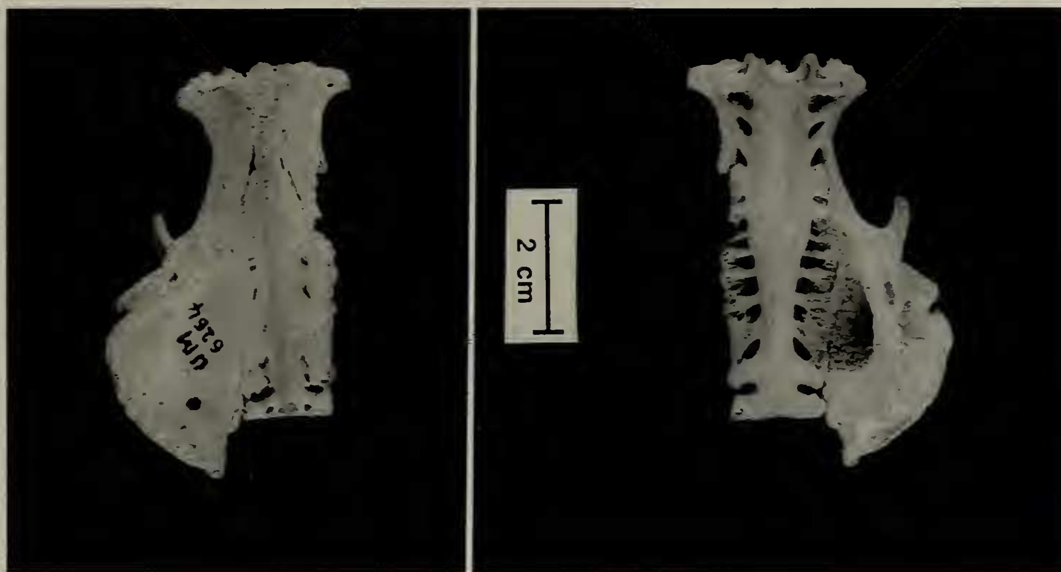

Fig. 1. Pelvis of *Coua berthae,* new species, holotype UM 6264, (left) dorsal and (right) ventral views.

léontologie des Vertébrés, Service de Paléontologie, Université d'Antananarivo, UM 6264 (Figs. 1, 2). Collected during the 1983 field season.

Locality.—From surface deposits, Grotte d'Anjohibe (Andranoboka), Grotte Principale no. 1 (de Saint-Ours & Paulian 1953), Fivondronana (subprefecture) of Mahajanga, Province of Mahajanga, about 80 km NE Mahajanga, Madagascar (coordinates: 1) Laborde system—X = 1172, y = 448 and 2) 15°32′S, 46°53′E).

Chronology.—No radiometric date is available from the site. Presumed to be Quaternary, probably Holocene.

Measurements of holotype.—Length—from cranial border of the ilia to the Spinae iliocaudales, 68.2 mm; length along the vertebrae—from most cranial vertebra fused with the Os lumbosacrale to the most caudal vertebra fused with the Os lumbosacrale, 58.1 mm; smallest breadth across the Partes glutaeae of the ilia, 18.3 mm; and greatest breadth across the Partes glutaeae of the ilia, 29.2 mm. (See von den Driesch, 1976, fig. 59a, c for illustrations and descriptions of these measurements.)

Etymology.—Named in honor of Madame Berthe Rakotosamimanana, Directeur du Laboratoire d'Anthropologie, and Professor, Service de Paléontologie, Université d'Antananarivo, who for many years has helped students and foreign researchers working on Madagascar in the fields of paleontology and zoology, and also for her contribution to these disciplines.

Diagnosis.—Distinctly larger than any extant member of the genus *Coua* (Table 2). On the basis of a regression analysis of pelvic and tarsometatarsus measurements (see Discussion), *C. berthae* is larger than *C. delalandei,* a large recently extinct ground-dwelling species; *C. primavea,* an undated fossil species only known from a single tarsometatarsus; and all living *Coua* spp.

Paratype.—Complete tarsometatarsus, Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris, MAD 5490, collected at Ampasambazimba in 1911 by A. Grandidier and presented as a gift of the Academie Malgache.

Measurements of paratype.—Total length, 92.9 mm; proximal width 12.4 mm; and distal width 13.1 mm.

Discussion.—Within the four extant couas (*C. caerulea, reynaudii, ruficeps,* and *cristata*) for which there was more than one skeletal specimen of each available for study, there is little intraspecific variation in three pelvic measurements and in the greatest

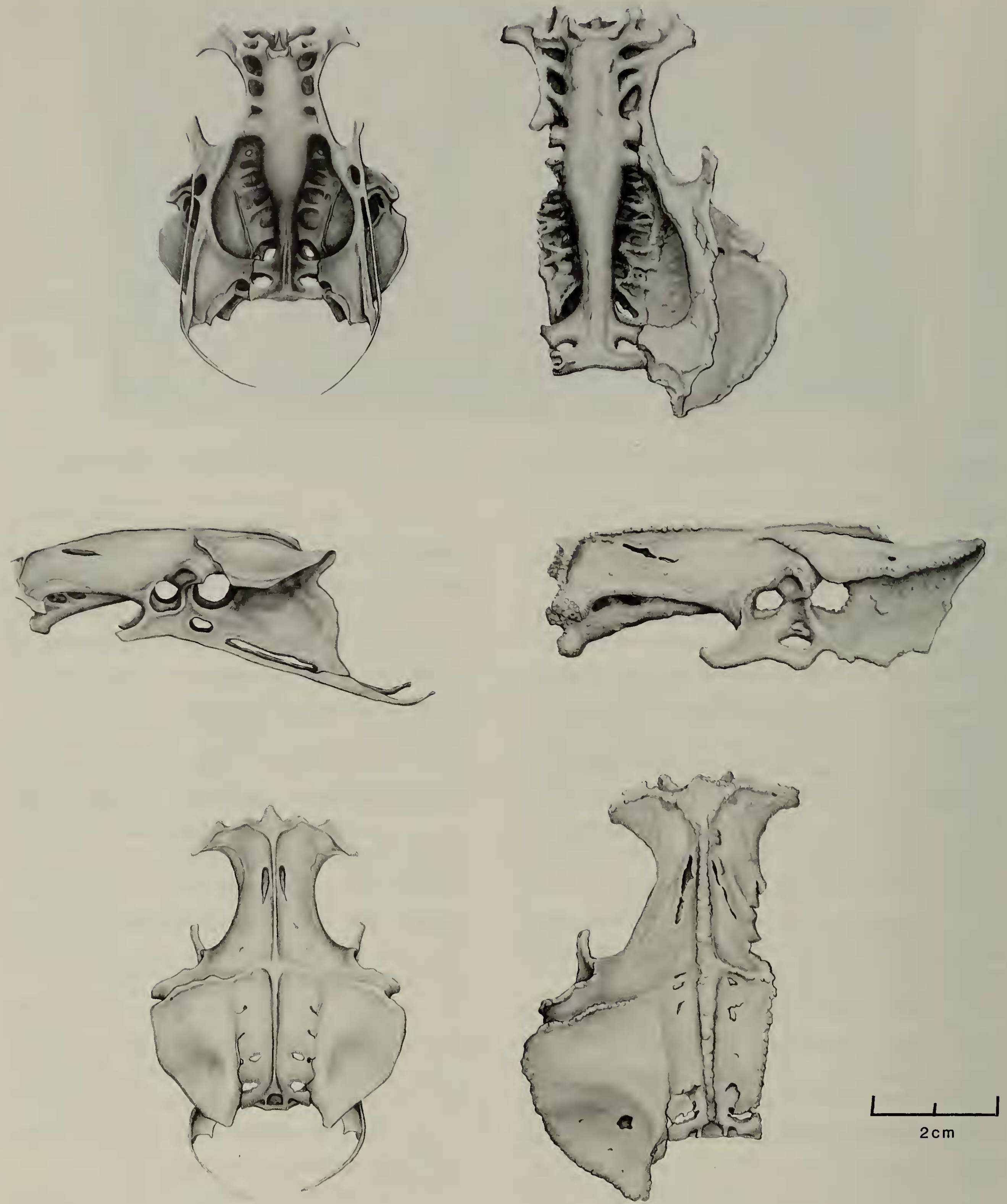

Fig. 2. Comparison of *Coua gigas* (FMNH 345635) pelvis (left) and *Coua berthae* (UM 6264) pelvis (right). The three views from the top are ventral, left lateral, and dorsal.

length of the tarsometatarsus (Table 2). *C. cristata* shows some geographic variation in size (Milon 1950), which accounts for the greater variability in the range of these measurements in this species than the other three. Within these four species there is no discernable sexual dimorphism in the skeletal measurements. A strong linear rela-

Table 2.—Pelvis and tarsometatarsus measurements (mm) of *Coua* spp.

	Pelvis				Tarsometatarsus
Species	Length[1]	Length along the vertebrae	Cranial breadth	Smallest breadth of ilia	Greatest length
berthae, sp. nov.[2]	68.2	58.1	~29.2	18.3	92.9
primavea	[62.5]	—	—	—	83.2[3]
gigas (n = 1)	49.3	42.3	25.8	12.5	68.7
caerulea	44.28	38.70	24.20	13.75	55.20
	n = 5	n = 6	n = 5	n = 6	n = 5
	(42.0–45.8)	(37.3–40.1)	(23.6–24.7)	(13.3–14.0)	(53.1–58.0)
cristata	33.30	29.10	17.44	10.29	42.96
	n = 7	n = 7	n = 5	n = 7	n = 5
	(30.2–36.5)	(26.8–29.8)	(15.6–19.0)	(9.4–11.6)	(39.3–47.8)
reynaudii	35.98	31.33	17.78	9.80	47.60
	n = 4	n = 4	n = 4	n = 4	n = 3
	(35.3–36.8)	(30.1–32.3)	(17.2–18.6)	(9.7–11.2)	(46.4–48.4)
ruficeps	40.15	32.28	21.05	10.97	57.68
	n = 6	n = 6	n = 6	n = 6	n = 5
	(39.3–40.8)	(30.6–34.3)	(20.4–21.6)	(9.8–11.8)	(55.2–60.2)
serriana (n = 1)	45.9	37.6	22.6	13.3	61.0

[1] See text p. 27 for definitions of pelvis measurements. Measurement in brackets is inferred on the basis of a regression analysis.

[2] *C. berthae* pelvic measurements from type specimen, Service de Paléontologie, Université d'Antananarivo, UM 6264; and tarsometatarsus from Muséum National d'Histoire Naturelle, Service de Paléontologie, Paris, MAD 5490.

[3] Muséum National d'Histoire Naturelle, Service de Paléontologie, Paris, registration MAD 7078. Milne-Edwards & Grandidier (1895) gave the greatest length measurement of this element as 84 mm.

tionship exists among six *Coua* spp., for which at least one skeleton of each was available, between the lengths of the pelvis and of the tarsometatarsus (r^2 = 0.80), and species with multiple specimens form distinct clusters (Fig. 3). On the basis of this relationship, the point at which the 83.2 mm *primavea* tarsometatarsus intersects the regression line corresponds to a pelvic length of approximately 62.5 mm. Similarly, the *berthae* pelvis length of 68.2 corresponds to a tarsometatarsus length slightly larger than 90 mm (Fig. 3). Thus, by extrapolation, the *primavea* tarsometatarsus and the *berthae* pelvis are not the same taxon.

Further evidence for the distinction between *C. berthae* and *C. primavea* comes from a tarsometatarsus recovered at the famous subfossil lemur site of Ampasambazimba on the High Plateau. This element, the paratype of *C. berthae,* measures 92.9 mm, close to the length predicted by the regression analysis (Fig. 3). Moreover, the Ampasambazimba tarsometatarsus is 9.7 mm larger than the type of *C. primavea.* This difference is greater than any size variation found within extant *Coua* spp. (Table 2).

Coua delalandei, a species that has gone extinct in the past 150 years, has the longest tarsometatarsus of any known recent *Coua.* It is represented by less than 15 skin specimens in museums, and no skeletal material is available. The tarsometatarsus length of this species, as measured from museum skins, is 70 mm (Milne-Edwards & Grandidier 1895), considerably smaller than the tarsometatarsus measurement of *primavea* or *berthae.*

In numerous groups of cursorial birds there is an outgrowth of the ischium into a prominent tuberculum preacetabulare

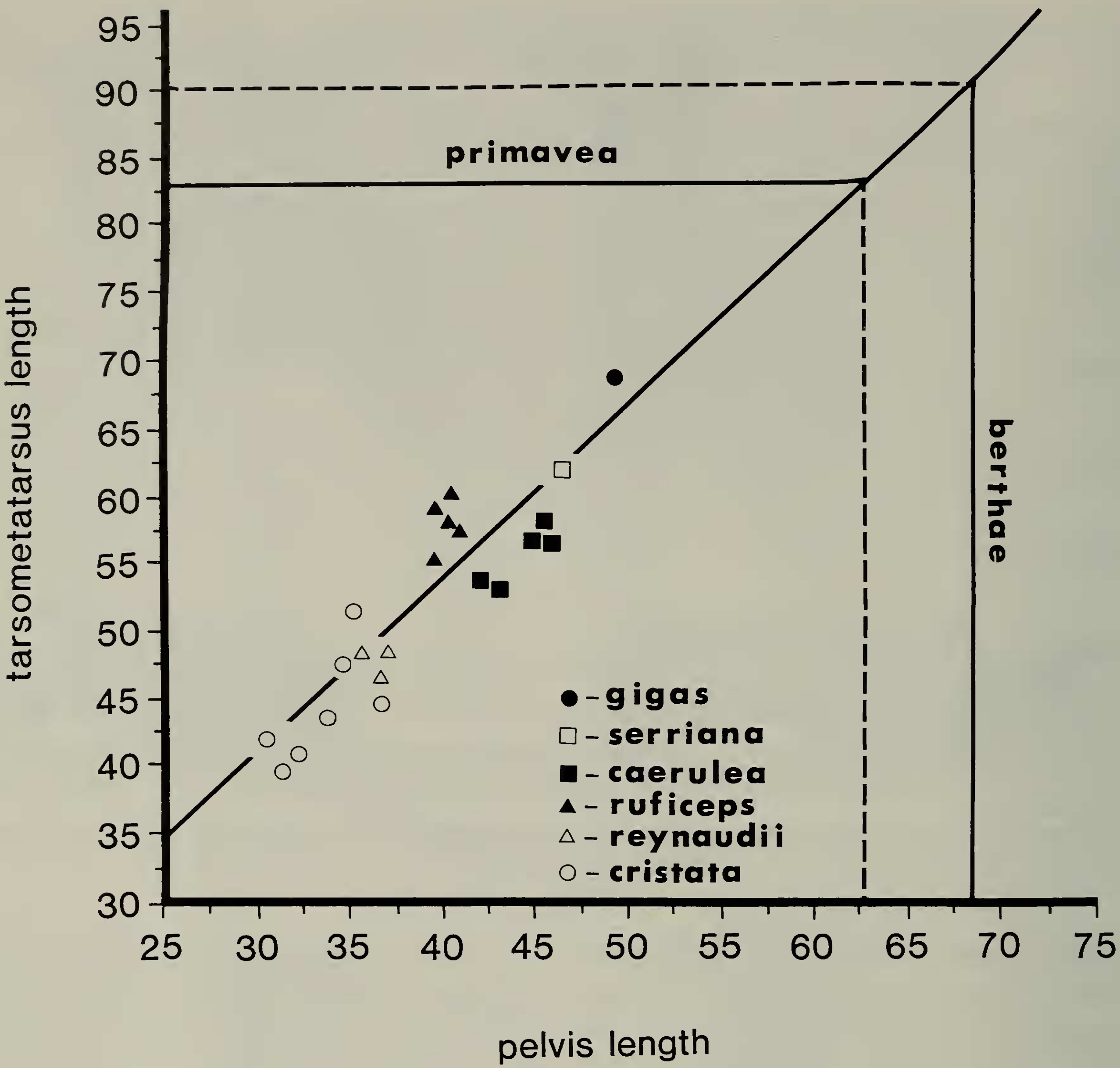

Fig. 3. Plot of tarsometatarsus length versus pelvis length in six species of modern *Coua*. The linear regression equation is y = 2.13 + 1.29x ($r^2 = 0.80$). Dotted lines are extrapolations of measurements based on the regression analysis.

(=pectineal process), the place the M. ambiens arises (Baumel 1979). In ground-dwelling cuckoos there is considerable development of this process and the M. abiens is present; this muscle is thought to help with the "facility of leg movement in running" (Berger 1952, 1953). In *gigas*, a terrestrial swift-running species and the largest extant *Coua* spp., the tuberculum preacetabulare is prominent. Absolutely and proportionately, this process as well as the antitrochanter is larger in *berthae* than *gigas* (Fig. 2), and the former was presumably an extremely large and swift-running species of *Coua*.

Weights are available for seven of the modern skeletal specimens measured, representing *gigas, caerulea* (3), *cristata,* and *reynaudii* (2). When weight is regressed against length of pelvis, a clear relationship emerges, which is best explained by a logarithmic curve (Fig. 4, $r^2 = 0.97$). However, since this curve abruptly flattens out, the point at which the *berthae* pelvis measurement would intersect the regression line is at an exceptionally heavy weight. A more

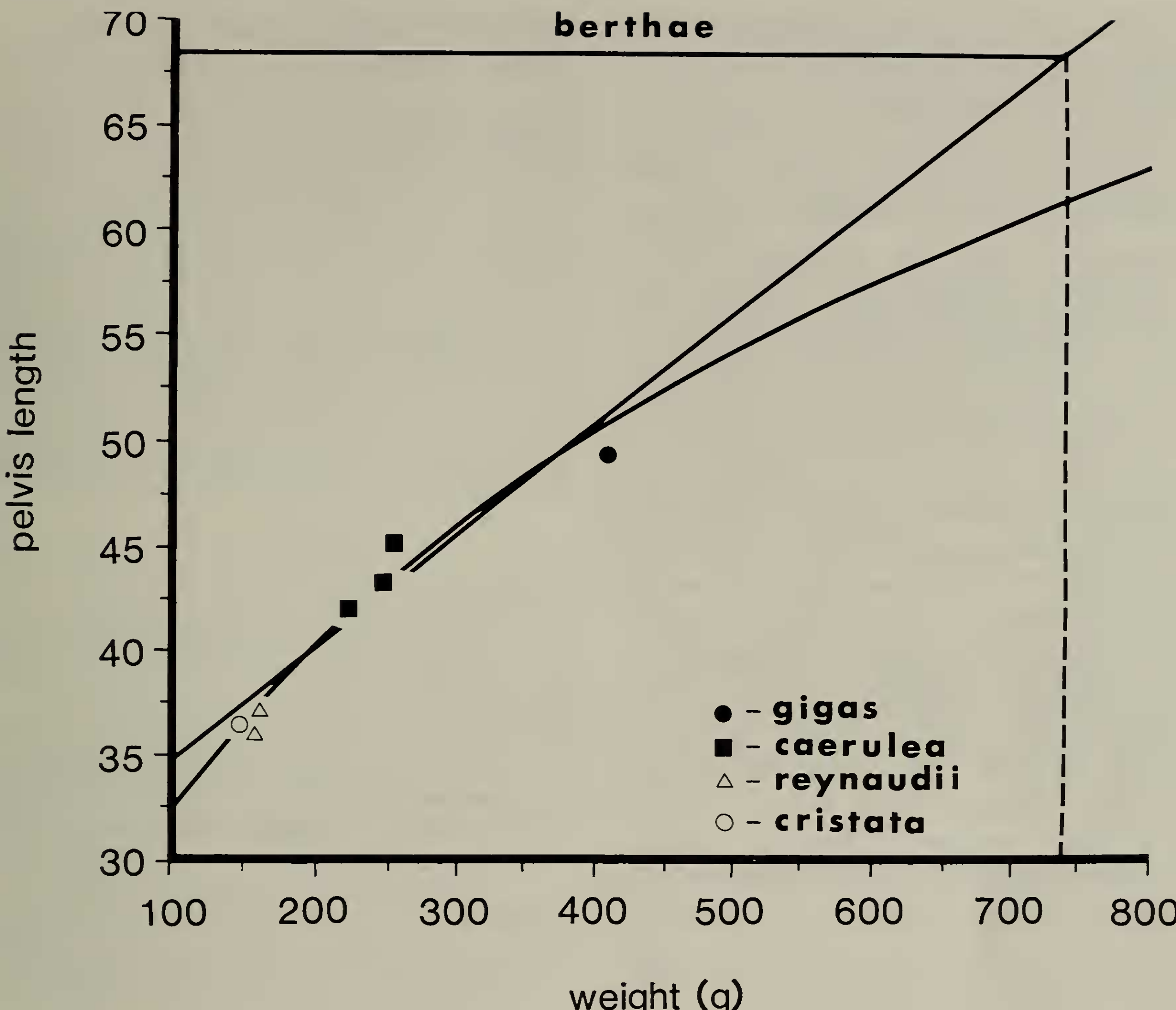

Fig. 4. Plot of pelvis length versus body mass in four species of *Coua*. The two regression lines are based on linear and logarithmic analyses. The dotted line is the extrapolation of *Coua berthae*'s mass based on the linear regression analysis.

conservative approach is to examine the same relationship with linear regression (Fig. 4, $r^2 = 0.92$), and thus by extrapolation, the pelvis length of *berthae* would intersect this curve at about 740 g, which is the presumed approximate minimum weight of this species. Since no portion of the sternum or wing bones of *berthae* is known, it is impossible to determine if this species was volant. However, given its considerable body mass and that all *Coua* spp. have proportionately small wing bones (Milne-Edwards & Grandidier 1879, Berger 1953), at the very least *berthae* almost certainly was not a strong flier.

In modern Madagascar, terrestrial *Coua* spp. are regular victims of human trapping and hunting (Langrand 1990), and this is one of the causes that has been proposed for the demise of *C. delalandei.* During an unsuccessful search in April 1991 of the remaining forests of Ile St. Marie for a remnant population of *C. delalandei,* it was found that there is still exploitation of wild animals and that *C. caerulea* is extensively hunted (Goodman, 1993). Although tempting to infer human involvement, it is premature to make any suppositions on when and why *Coua berthae* went extinct. The study of bird material already recovered from sites and new excavations with detailed stratigraphic control should elucidate some of the missing information on the number and timing of Quaternary bird extinctions on Madagascar.

Comparative material examined.—Osteological material of *Coua* spp. is rare in collections and skeletons of *C. delalandei, coquereli, cursor,* and *verreauxii* are not available for comparison. With the exception of *delalandei,* all of these birds are small species, and the absence of comparative material did not hamper the analysis. The pelvis of *C. berthae* was compared to modern skeletal material of the following *Coua* spp. (see Acknowledgments for definitions of acronyms): *gigas* (FMNH 345635; UM uncataloged partial specimen), *caerulea* (AMNH 6429, 10070; FMNH 345642, 345644, 352802; UM four uncataloged partial specimens; UMMZ 209201), *cristata* (AMNH 6430, 10071; MNHN 1883-512, 1883-514, 1883-517; FMNH 345639; UMMZ 157526; USNM 432197, 432219, 432238), *reynaudii* (FMNH 352797, 352798; UMMZ 208403; USNM 208403), *ruficeps* (MNHN 1883-518, 1883-519, 1883-521, 1883-522, 1883-523; USNM 432195), and *serriana* (UMMZ 209202).

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